THE COMPARATIVE ANATOMY OF DIGESTIVE GLANDS IN THE FEMALE CASTES AND THE MALE OF *CAMPONOTUS PENNSYLVANICUS* DEGEER (FORMICIDAE, HYMENOPTERA).

JAMES FORBES and AUGUST MARTIN MCFARLANE, F.S.C.[1]

BIOLOGICAL LABORATORY, FORDHAM UNIVERSITY, NEW YORK 58, N.Y.

Three pairs of well developed glands are usually associated with the digestive system in ants: the maxillary glands, the postpharyngeal glands, and the salivary or labial glands. These glands have been described for some of the forms of several formicine and myrmicine ants by Meinert (1861), Lubbock (1877), Nassonow (1889), Janet (1894, 1897, 1898, 1904, 1905 and 1907), Bugnion (1930), and Forbes (1938). More recently descriptions of these glands have been made for two social parasitic ants, *Teleutomyrmex schneiderei* (Gösswald, 1953) and *Anergates atratulus* and its host, *Tetramorium caespitum,* (Meyer, 1955). Whelden (1957 a and b) has described the glands in two ponerine species.

The digestive glands in the queen and the male of the black carpenter ant, *Camponotus pennsylvanicus* DeGeer, have not been previously reported, nor have the size of the glands been compared in the different-sized workers. This paper is a comparative study of the anatomy of the digestive glands in the female castes and the male of this polymorphic species. In addition, comparisons have been made of all observations on these glands so far reported; since the queens, the workers, and the males have different functions within the colony, these comparisons may help toward an understanding of the functions of the glands.

MATERIAL AND METHODS

The specimens used in this study were collected in Westchester County, New York during July of 1936 and in Nassau County, New York during February 1953 and March 1954. The specimens taken in 1936 were fixed in alcoholic Bouin's fluid, those taken in 1953 in Kahle's fluid, and those taken in 1954 in 10 per-

[1] Present address: St. Joseph's Boys High School, West New York, N.J.

cent formalin. The material in Bouin's fixative was stored in 80 percent alcohol and the materials fixed in Kahle's fixative and in formalin were stored in 70 percent alcohol. All the queens used in this study were virgin, unmated queens.

The dissections were performed in Syracuse watch glasses, which had a thin layer of paraffin on the bottom. The specimens were placed in grooves on the paraffin surface and held in place by melting paraffin around them. They were then covered with 70 percent alcohol. The maxillary and the post-pharyngeal glands together with the anterior portion of the alimentary tract were removed as a unit. The salivary glands were separated from muscle and other surrounding tissues and they, too, were removed almost completely intact. These organs were stained with either Grenacher's borax-carmine or by Lynch's precipitated borax-carmine method (Galigher, 1934). In the organs stained with Grenacher's borax-carmine, it was observed that the stain was not retained in those structures which have a chitinous lining, but the other structures such as the maxillary gland cells were stained in a very satisfactory manner. For the purpose of studying the post-pharyngeal and salivary glands Lynch's precipitated borax-carmine method was found more suitable. The stained material was then dehydrated in ethyl alcohol and mounted in diaphane.

A Bausch and Lomb Tri-Simplex microprojector was used in preparing the drawings.

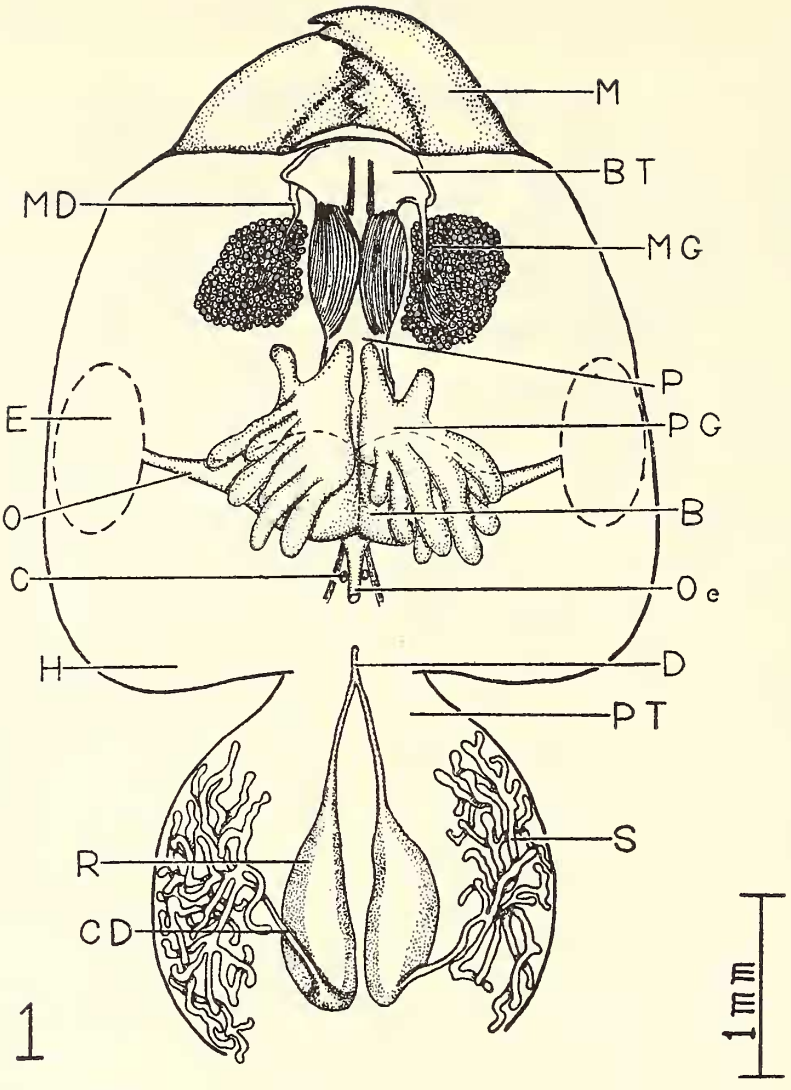
OBSERVATIONS

General Description of the Glands

The maxillary glands consist of two groups of cells which lie close to and on either side of the pharynx near the infrabuccal

Explanation of Plates

Figs. 1–5. Diagrams of dorsal dissections of the head and prothorax of the various *Camponotus pennsylvanicus* forms, all drawn to the same scale. 1. Large-sized worker, 2. Medium-sized worker, 3. Small-sized worker, 4. Male, 5. Queen. Abbreviations: A, apodeme; B, brain; BT, buccal tube; C, corpora allata; CD, collecting duct of salivary tubules; D, salivary gland duct; E. compound eye; FM, flight muscles; H, head capsule; L, labrum; M, mandible; MD, maxillary gland duct; MG, maxillary gland; O, optic nerve: Oe, oesophagus; P, pharynx; PG, post-pharyngeal glands; PT, prothorax; R, salivary gland reservoir; S, salivary gland tubules.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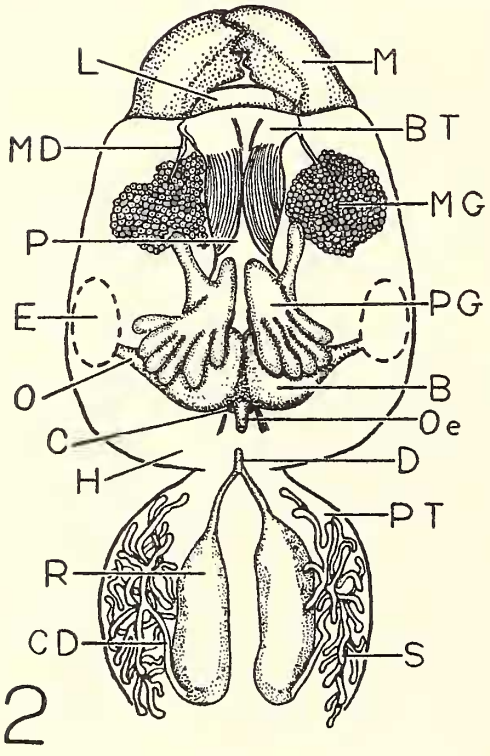
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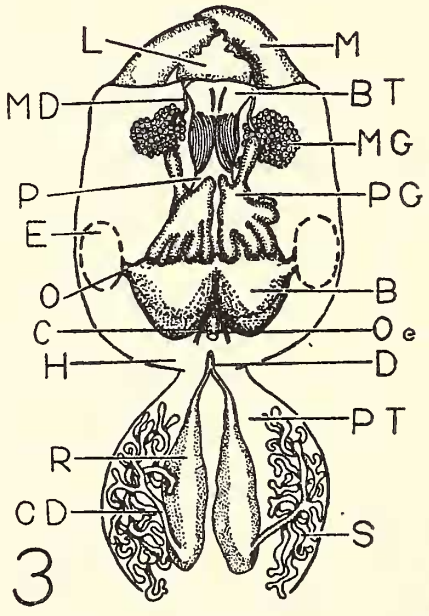
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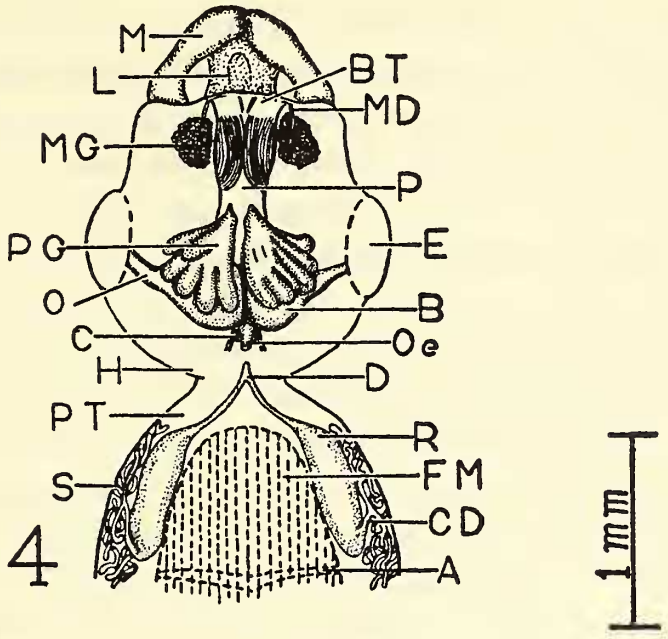
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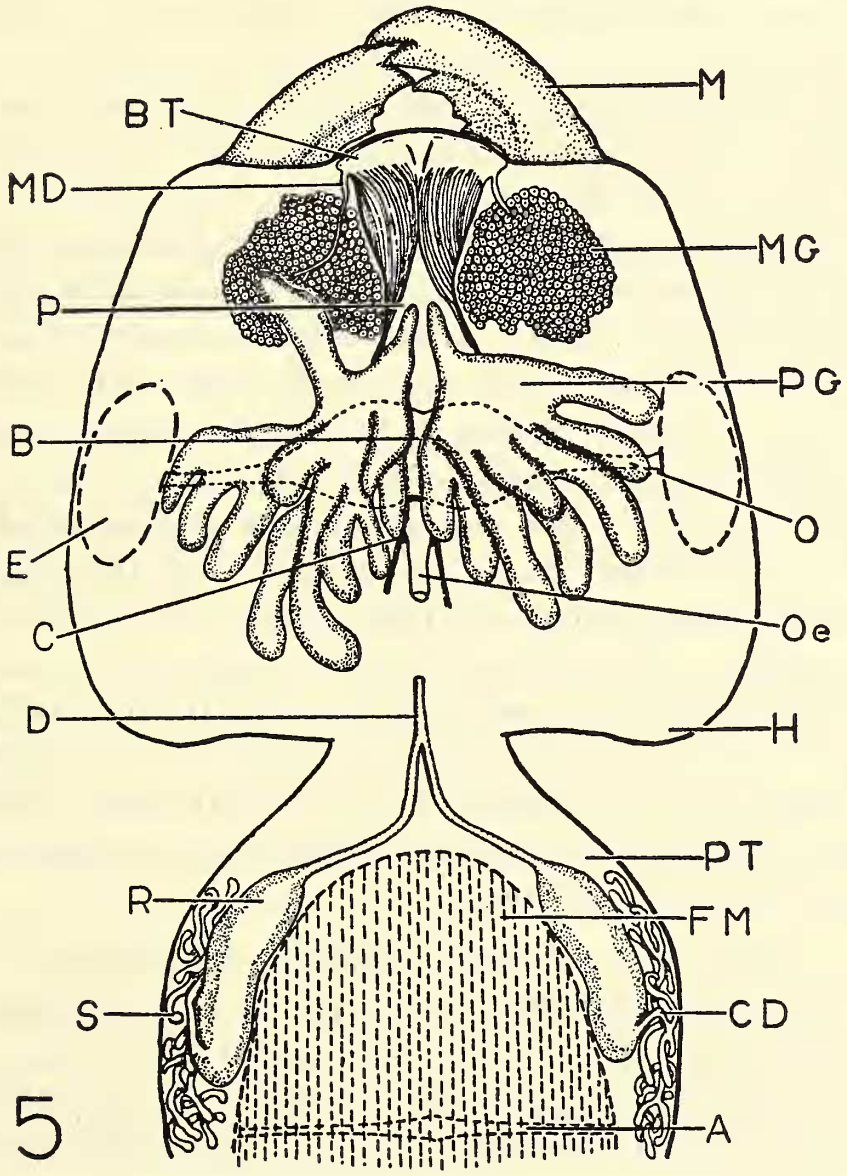
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chamber. They extend laterally into the head cavity (fig. 1). The large gland cells contain large, centrally located nuclei. When free from the pressure of surrounding cells, these gland cells are spherical or oval-shaped; however, because of the number of cells in the glands, the shape is usually determined by mutual compression of the surrounding cells. Each cell is drawn out on one side to form a single, slender duct. The cell ducts of each gland unite to form a main duct. These ducts continue forward and open on the posterior lateral margins of the buccal tube.

The post-pharyngeal glands are a pair of branched, tubular-shaped glands which arise from the dorsal, posterior region of the pharynx (fig. 1). These are the largest glands found in the head. Most of the finger-like tubes extend posteriorly and lie over the brain, some extend anteriorly and almost parallel to the pharynx, while others extend laterally. A few tubes usually extend downward around the anterior part of the brain. The tubes of each gland are arranged in a fan-like fashion with the tubes uniting at the base. Each gland then opens separately on the dorsal, posterior portion of the pharynx.

The salivary or labial glands are situated in the dorsolateral regions of the prothorax (fig. 1). They consist of two groups of thin-walled, multibranched tubules which extend forward to the anterior wall of the prothorax and posteriorly to the mesothorax. Some of the glandular tubules lie between the muscles of the prothorax. The branched tubules of each gland unite to form a single duct, which opens into the posterior end of a thin-walled, dilated reservoir. The reservoirs lie ventromedially to the glands. The narrow duct which leads from the anterior end of each reservoir bends ventrally. These ducts lie one on either side of the oesophagus. They unite in the neck region under the longitudinal connectives of the ventral nerve cord to form one median duct. This single, salivary duct continues into the ventral side of the head, it passes under the brain and the infrabuccal sac, and it opens on the upper side of the labium.

CASTE AND SEX DIFFERENCES OF THE GLANDS

MAXILLARY GLANDS. The size of the maxillary glands differs in the small-sized, medium-sized, and large-sized workers (figs. 1, 2 and 3). The glands and the gland cells in the large-sized workers are larger, for the most part, than the glands and the majority

of the gland cells in the medium-sized workers. Similarly, the glands and the gland cells in medium-sized workers are generally larger than those in small-sized workers.

The maxillary glands of the queens are the largest. They occupy a large portion of the space in the head capsule anterior to the antennae (fig. 5). A greater number of cells and also an increase in the size of the individual cells account for this increased size of the maxillary glands in the queens. While some of the cells are small and may be even smaller than the large cells found in the large-sized workers, most are about one and a half times the size of those in the large-sized workers.

In the males,there is a reduction in the cell size and a noticeable reduction in the size of the maxillary glands (fig. 4). The glands and their cells are even smaller than those in the small-sized workers.

Post-pharyngeal glands. The post-pharyngeal glands in the different-sized workers are limited to the region of the brain (figs. 1, 2 and 3). In some individuals, a few of the glandular tubes may extend laterally and cover the optic nerves. In the large-sized worker the tubes extend slightly beyond the posterior border of the brain. In the medium-sized worker the tubes extend past the mid-section of the brain and a few of the lateral tubes may extend to the posterior border of the brain. In the small-sized worker only the anterior part of the brain is covered by the glandular tubes. There is no fat tissue around these glands in any of the workers.

The post-pharyngeal glands of the queens occupy a much greater portion of the head capsule than do those of the workers (fig. 5). In the queens, the tubes are larger and longer than in the workers; they cover the brain and optic nerves completely and extend below the optic nerves as well as above them. Some of the dorsally situated tubes extend almost to the posterior wall of the head capsule. Some of the laterally situated tubes extend to the eyes. Considerable fat tissue covers the gland and is situated between the individual glandular tubes.

In the males, the tubes extend beyond the mid-section of the brain (fig. 4) and they are a little larger than those in the small-sized workers. A fair amount of fat tissue is found in the head of the male. As is the case in the queen, fat tissue lies between the individual tubes of these glands.

The above observations of the post-pharyngeal glands in the various forms indicate the size of the glands in relation to the size of the brain. Another approach is a comparison of the size of the glands to the head size (the figures indicate this relationship). On this basis, the post-pharyngeal glands of the queen are again the largest. Again for the workers, there is a slight decrease in gland size from large-sized workers to small-sized workers. The size of the glands in the male falls between that of the medium- and small-sized workers; however, there is very little difference in these last three forms.

SALIVARY GLANDS. In the small-sized, medium-sized, and large-sized workers, the salivary glands are well developed (figs. 1, 2 and 3). A large number of branched, glandular tubules are distributed along the entire length of the dorsolateral region of the prothorax, and a number of tubules continue dorsomedially from each side. A few of the posterior tubules are found in the anterior, lateral portion of the mesothorax. The reservoirs are large, they lie side by side in the median portion of the prothorax, and they run the entire length of the prothorax in all members of this caste. Usually, the posterior ends of the reservoirs extend into the mesothorax.

The salivary gland tubules of the queens are fewer in number than in the workers (fig. 5), and the reservoirs are comparatively smaller than those of the workers. The reservoirs are arranged close to the lateral walls of the prothorax, they are shifted anteriorly and to the side because of the well developed wing muscles in the mesothorax, and they lie completely within the prothorax.

The males, like the queens, show fewer tubules than the workers. The position of the tubules and the reservoirs is similar to that in the queens (fig. 4). The reservoirs in the males are smaller than those found in the small-sized workers.

DISCUSSION

The maxillary glands, the post-pharyngeal glands, and the salivary glands are present in the female castes and the male of *C. pennsylvanicus*. The sizes of these glands differ somewhat for the various forms.

The maxillary glands of the queens and workers of *Camponotus maculatus oasium, C. vagus, Cataglyphis bicolor, Oecophylla*

smaragdina, and *Atta sexdens* studied by Bugnion (1930) and the *C. pennsylvanicus* workers (Forbes, 1938) are similar in their size, position, and arrangement to the glands of the queens and workers observed in this study. However, a different arrangement of the ducts of these glands has been described for *Formica rufa, F. fuliginosa,* and *Myrmica ruginodis* (Meinert, 1861), for *F. rufa, M. rubra,* and *Lasius niger* (Janet, 1894, 1899, and 1905), for *L. flavus, L. niger,* and *M. ruginodis* (Lubbock, 1877), and for *Stigmatomma pallipes* and *Rhytidoponera convexa* (Whelden, 1957 a and b). In these species the individual gland cell ducts open separately on a small cribellum at either side of the buccal tube. Each cribellum opens into a short collecting duct. Maxillary glands are completely lacking in the queen of the parasitic ant, *Teleutomyrmex schneiderei* (Gösswald, 1953); these glands are lacking in both the queens and the males of *Anergates atratulus,* but they are present in all forms of this latter's host ant, *Tetramorium caespitum* (Meyer, 1955).

The post-pharyngeal glands in *F. rufa* workers (Meinert, 1861 and Janet, 1894) appear larger and seem to have more tubes and longer tubes than those observed in *C. pennsylvanicus.* Janet (1894) states that some of these tubes descend in front of the brain but the greater portion is stretched out above the brain; this is also true for *C. pennsylvanicus.* The post-pharyngeal glands of *M. ruginodis worker* (Meinert, 1861), *L. mixtus* worker, *L. niger* queen, and *M. rubra* worker (Janet, 1897, 1899, and 1905), and *C. bicolor* and *O. smaragdina* workers (Bugnion, 1930) correspond in size to these glands in the workers and queens of *C. pennsylvanicus.* The post-pharyngeal glands as pictured by Lubbock (1877) in *L. niger, L. flavus,* and *M. ruginodis* and in the workers of *L. flavus* (Nassonow, 1889) are likewise similar to those found in *C. pennsylvanicus.* Bugnion (1930) found these glands in the *Messor structor* queens to be completely different in form and extent. *Atta sexdens* queens have much smaller glands, *C. vagus* queens have somewhat smaller glands, and the glands of *C. maculatus oasium* workers are much larger than the glands in the female castes of *C. pennsylvanicus.*... The previous description of these glands in *C. pennsylvanicus* workers (Forbes, 1938) agrees with the observations made for this caste in this study. Whelden's description of these glands in both *Stigmatomma pallipes* (1957 a) and *Rhytidopnera convexa* (1957 b) is similar to

that for *C. pennsylvanicus;* in *S. pallipes,* the tubules of these glands are larger and more numerous in the queens and smaller and fewer in the males than they are in the workers. Meyer (1955) reports these glands as normal in *Anergates atratulus* and its host, *T. caespitum.* In *T. caespitum* queen, they fill a large part of the head. Gösswald (1953) observed that the glands in the *Teleutomyrmex schneiderei* queen were smaller than those found in *T. caespitum.*

Meinert's (1861) illustration of the salivary glands of *F. rufa* worker is similar to the observation for *C. pennsylvanicus.* The number of tubules appears to be fewer than in *C. pennsylvanicus* worker. The location of the salivary glands in *M. rubra* queen and worker, in *L. niger* queen (Janet, 1898, 1899, 1904, 1905 and 1907), and in *C. pennsylvanicus* worker (Forbes, 1938) agrees with the present observations; however, the *M. rubra* queen and worker do not have salivary reservoirs. Gösswald (1953) reports these glands are reduced to a small, blind sac situated on the dorsal side of the oesophagus in *Teleutomyrmex schneiderei,* and Meyer (1955) observed in *A. atratulus* only occasional gland cells in the prothorax and no distinct excretory duct. In both *Stigmatomma pallipes* and *Rhytidoponera convexa* (Whelden, 1957 a and b), the glands are located in the ventral region of the thorax, and salivary reservoirs are absent. The salivary duct in *S. pallipes* appears fairly straight externally, but it has a long, twisted, folded central canal. In *R. convexa,* isolated fragments of the glands were found in the gaster. The salivary ducts in some individuals of this species travel forward separately in the head to the mouth while in others they unite in the neck region to form a single duct. These glands are reduced in the male of *R. convexa.*

Very little is really known about the activities of the glands studied in this paper although glands which are connected to or associated with the digestive tract are assumed to be digestive in function. Secretion vacuoles have been seen in the cytoplasm of maxillary gland cells (Forbes, 1938; Whelden, 1957 a and b); however, in the parasitic ants investigated by Gösswald (1953) and Meyer (1955) the maxillary glands are lacking. Thus, it might be assumed that, in addition to serving a digestive function, these glands may also play some part in trophallaxis. The postpharyngeal glands are present in all the ants so far investigated. Bugnion (1930) observed from his numerous dissections that the

pharynx and pharyngeal glands in the more primitive ants (ponerines and dorylines) were not as well developed as in the higher forms (camponotines, formicines, and myrmicines). He concluded that the better development in the case of the higher forms resulted from the feeding of the larvae by regurgitation, which he assumed the primitive forms did not do. Recent developments do not uphold this conclusion. It is now known that there is a transfer of ingluvial food from adults to larvae in some species of ponerines and even in two species of the primitive *Myrmecia* (Haskins and Whelden, 1954). On the other hand, these investigators have not observed this activity in the ponerine, *Stigmatomma pallipes,* although the post-pharwngeal glands are well developed, particularly in the female castes (Whelden, 1957 a). Janet (1897) observed that colored honey fed to workers of *Lasius mixtus* moved into some of the tubules of these glands and then left the tubules as more uncolored honey was fed to the workers. Secretion granules have been reported in the cytoplasm of the cells of these glands (Bugnion, 1930; Forbes, 1938; Whelden, 1957 a and b), and Bugnion suggested that a nutritive substance was added at the moment of disgorgement. On the basis of Janet's observation and considering that these glands are present in all ants, a better suggestion might be that a substance which aids in digestion is added when the food is taken in. These glands probably serve the digestive activities of the individual ant.

The salivary glands are not present in the two species of parasitic ants investigated, but they are present in all other species. These glands are well developed in the female castes and less well developed in males. They are best developed in the worker castes in *C. pennsylvanicus.* Bernard (1951) believes these glands are probably concerned with feeding the larvae and rearing the brood and that they might produce a specific nutrient material. These observations indicate that these glands may play an important role in trophallaxis.

SUMMARY

1. The anatomy of the maxillary glands, the post-pharyngeal glands, and the salivary glands is described for the female castes and the male of the black carpenter ant, *Camponotus pennsylvanicus.*

2. The maxillary glands and maxillary gland cells differ somewhat in size in the queen, the workers, and the males. The size decreases in the following order: queen, large-sized worker, medium-sized worker, small-sized worker, and male.

3. The post-pharyngeal glands attain a remarkably large size in the queen and occupy most of the head capsule. In the workers there is a slight reduction in the gland size from the large-sized worker to the medium-sized worker, and again to the small-sized worker. The size of the glands for the male lies between that of the medium-sized worker and the small-sized worker. Fat tissue covers the glands in both the queen and the male.

4. The salivary glands in all three types of workers show well developed reservoirs and a large number of tubules. In the queen and the male there is a reduction in size of the reservoir and also in the number of tubules present.

5. Comparisons are made between the glands in *Camponotus pennsylvanicus* and the other reported genera and species.

6. All these glands probably serve a digestive function for the individual ants. The maxillary and salivary glands may play an important role in trophallaxis.

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